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We have realistically modeled the two-eye visual environment. We study how
orientation selectivity and ocular dominance form simultaneously. In particular,
we study the effect of image misalignment between the two eyes on receptive field
formation. We have compared how image misalignment affects receptive fields under
two different learning rules PCA in the form proposed by Oja in 1982 and BCM. We
have chosen to examine these two because they are well defined and have stable fixed
points. We have shown that binocular misalignment has very different effects on
these two learning rules. For the BCM learning rule misalignment is sufficient to
produce varying degrees of ocular dominance, whereas for the PCA learning rule
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2

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1 Comparison of BCM and PCA learning in a realistic Binocular Environment

Different models, that attempt to explain how cortical receptive fields evolve, have been proposed over the years Typically these models are distinguished by their learning rule, the representation of the visual environment, and the architecture of the network.

Most of these models assume a simplified representation of the visual environment or a second order correlation function of the visual environment Realistic representations of the visual environment have only very recently been considered

Recently we have realistically modeled the two-eye visual environment. We study how orientation selectivity and ocular dominance form simultaneously. In particular, we study the effect of image misalignment between the two eyes on receptive field formation

We have compared how image misalignment affects receptive fields under two two different learning rules PCA in the form proposed by Oja in 1982 and and BCM We have chosen to examine these two because they are well defined and and have stable fixed points.

We have shown that binocular misalignment has very different effects on these two learning rules. For the BCM learning rule misalignment is sufficient to produce varying degrees of ocular dominance, whereas for the PCA learning rule binocular neurons will emerge independent of the misalignment.

1.1 A Binocular Visual Environment Composed of Natural Images

We have used a set of 24 natural scenes. These pictures were taken at Lincoln Woods State Park and scanned into a 256 X 256 pixel image. We have avoided man-made objects, because they have many sharp edges, and straight lines, which make it easier to achieve oriented receptive fields.
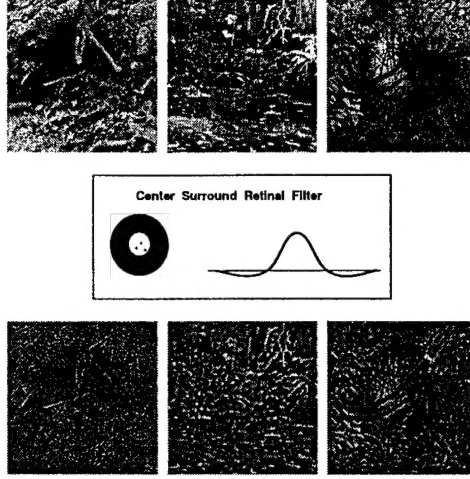
Figure 1: Three of the natural images used (top) processed by a Difference of Gaussians filter and presented at the bottom.

We have chosen to model the effect of the retinal preprocessing by convolving the images with a difference of Gaussians (DOG) filter, with a center radius of one pixel ($\sigma_1 = 1.0$) and a surround radius of three ($\sigma_2 = 3$)[1]. The effect of this preprocessing is shown in figure 1.

As illustrated in Figure 2, the input vectors from both eyes are chosen as small, partially overlapping, circular regions of the preprocessed natural images; these converge on the same cortical cell.
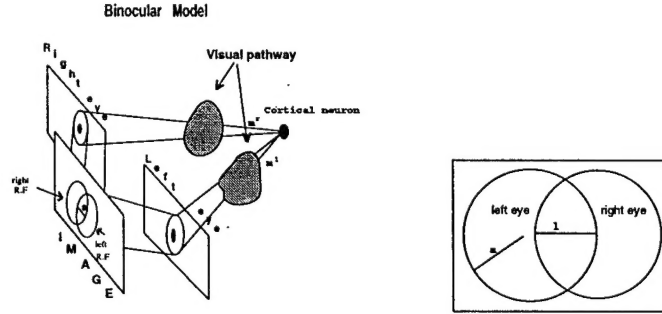

Figure 2: Schematic diagram of the two eye model, including the visual input preprocessing.

The input from the right and left eye respectively are denoted by $\mathbf{d}^l$ and $\mathbf{d}^r$, and the output of the cortical neuron then becomes $c = \sigma(\mathbf{d}^l \cdot \mathbf{m}^l + \mathbf{d}^r \cdot \mathbf{m}^r)$, where σ is the non linear activation function of each neuron. We have used a non-symmetric activation function to account for the fact that neuronal activity as measured from spontaneous activity has a longer way to go up than to go down to zero activity.

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[1]This ratio between the center and surround in biologically plausible, and enables the PCA rule to produce oriented receptive fields.

In order to examine the effect of varying the overlap between the receptive fields we define an overlap parameter $O = s/2a$, where a is the receptive field radius in pixels, and s is the linear overlap in pixels, as shown in Figure 2. When the left and right receptive fields are completely overlapping $O = 1$, when they are completely separate $O \leq 0$.

In order to assess the degree of cell binocularity, we introduced an ocular dominance measure B based on left and right eye response: $B = (L - R)/(L + R)$. B is calculated by first finding the orientation at which the cell has the greatest binocular response to a sinusoidal grading, and then measuring L and R, the left and right eye responses at that orientation.

1.2 Cortical plasticity learning rules

We have employed these realistic visual inputs to test two of the leading visual cortical plasticity rules that have been used to model various normal rearing and visual deprivation experiments: Principal components analysis (PCA) and the Bienenstock Cooper and Munro (BCM) model.

Principal components analysis (PCA) is one of the most widely used feature extraction methods for pattern recognition tasks. PCA features are those orthogonal directions which maximize the variance of the projected distribution of the data.

A simple interpretation of the Hebbian learning rule, is that with appropriate stabilizing constraints it leads to the extraction or approximation of principal components. This has often been modeled The learning rule that we use has been proposed by Oja (1982), and has the form: $\Delta m_i = \eta[d_i c - c^2 m_i]$ where d_i is the presynaptic activity at synapse i, c is the postsynaptic activity, and m_i is the strength of the synaptic efficacy of junction i. η, is a small learning rate. This learning rule has been shown to converge to the principal component of the data.

The BCM theory has been introduced to account for the striking dependence of the sharpness of orientation selectivity on the visual environment. We use a variation due to Intrator and Cooper (1992) for a nonlinear neuron with a non-symmetric sigmoidal transfer function. Using the above notation, the synaptic modification is governed by $\dot{m}_j = \eta \phi(c, \theta_M) d_j$, where the neuronal activity is given by $c = \sigma(m \cdot d)$, $\phi(c, \theta_M) = c(c - \theta_M)$, and θ_M is a nonlinear function of some time averaged measure of cell activity, which in its simplest form is given by $\theta_M = E[c^2]$, where E denotes the expectation over the visual environment. The transfer function σ is non symmetric around 0, to account for the fact that cortical neurons show a low spontaneous activity. The neuron can thus fire at a much higher rate relative to the the spontaneous rate, but can go only slightly below the spontaneous rate.

1.3 Results

In all the results reported here we used a fixed circular receptive field with a diameter of 20 pixels. We tested the robustness of the results to receptive fields of sizes 10 to 30 pixels and got no qualitative difference in the results.

BCM neurons acquire selectivity to various orientations in the partial and the non-overlapping case as well. When receptive fields are misaligned, various ocular dominance preferences may occur even for the same overlap. This result stands in sharp contrast to the one obtained by PCA neurons; only binocular neurons with a preferred horizontal direction emerge under for the PCA rule.
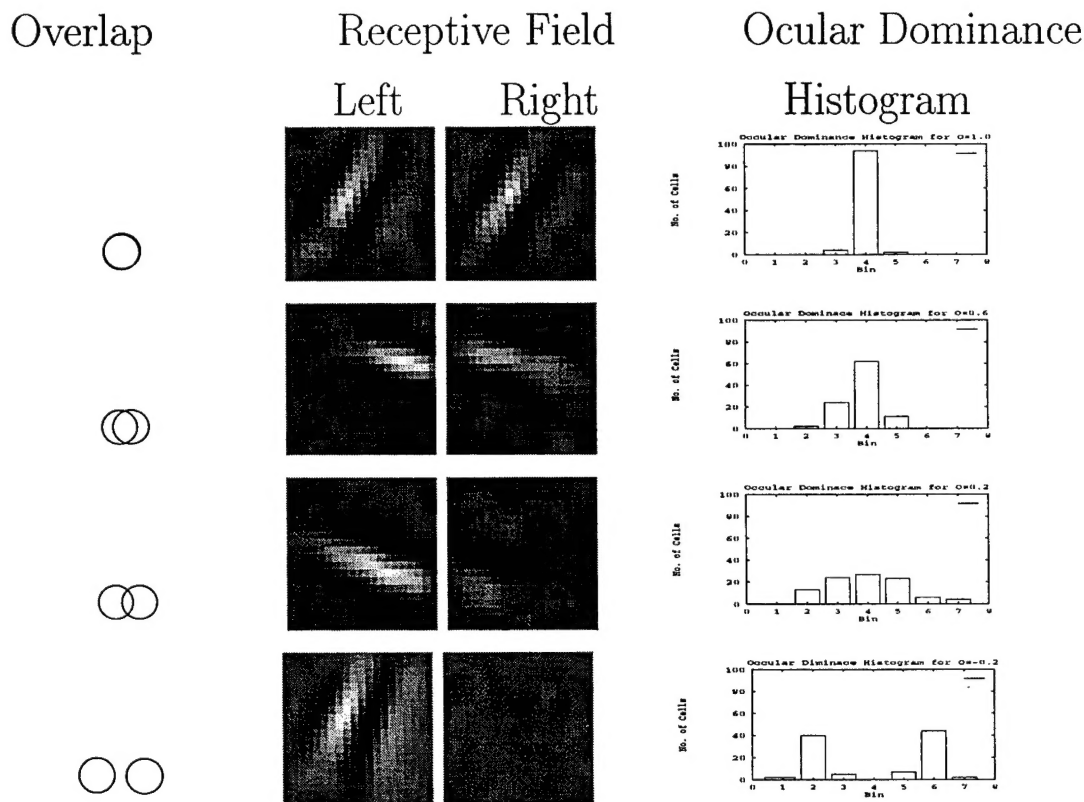

Figure 3: BCM neurons with different overlap values; $O = 1, 0.6, 0.2, -0.2$ from top to bottom. The ocular dominance histograms summarize the ocular dominance of 100 cells at each overlap value. The dependence of ocular dominance on visual overlap is evident.

The BCM receptive field formation results are summarized in Figure 3. Receptive field misalignment does not affect orientation selectivity of the dominant eye, but does produce varying degrees of ocular dominance; this depends on the degree of overlap between the receptive fields. The main result is that ocular dominance depends strongly (even for single cell simulations) on the degree of overlap between visual input to the two eyes.

The PCA results are presented in Figure 4. As mentioned above, it can be seen that the degree of overlap between receptive fields does not alter the optimal orientation, so that whenever a cell is selective its orientation is in the horizontal direction. The degree of overlap does affect the shape of the receptive fields, and the degree of orientation selectivity that emerges under PCA: orientation selectivity decreases as the amount of overlap decreases.
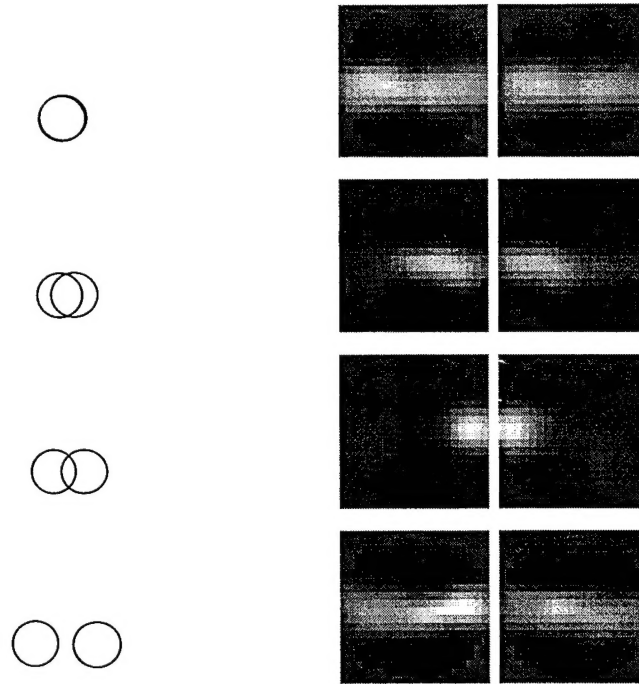
Figure 4: *Receptive fields for partially overlapping inputs using the PCA rule, Receptive field for an overlap value of O = .6 (top left). Receptive field for a small overlap, O = .2 (top right). Receptive field for no overlap , O = −.2 (bottom left). Receptive field for shift in the vertical direction between the visual inputs when O = .5 (bottom right). In all cases the cell is binocular and horizontal. The symmetry property evident in these receptive fields is analyzed in Shouval et. al. (1995).*

However, when there is no overlap at all, one again gets greater selectivity. For PCA, there is also a symmetry between the receptive fields of both eyes. This arises from invariance to a parity transformation that imposes binocularity.

We also studied the possibility that under the PCA rule, different orientation selective cells would emerge if the misalignment between the two eyes was in the vertical direction, but this produced horizontal binocular cells as well.

The PCA results described above were quite robust to the introduction of nonlinearity in cell's activity; there was no qualitative difference in the results when a non symmetric sigmoidal transfer function was used.

Thus we conclude that in a realistic visual environment the BCM neuron develops orientation selective cells to all orientations, as well as varying ocular dominance. This is consistent with observation. In contrast the PCA neuron is unable to develop cells selective to all orientations and the cells are always binocular, which is not in agreement with observation.

Role of the visual environment in the formation of receptive fields according to the BCM theory

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Introduction

Modification of synaptic effectiveness between neurons in cortex is widely believed to be the physiological basis of learning and memory; further, there is now evidence that similar synaptic plasticity occurs in many areas of mammalian cortex (Kirkwood et al., 1992). In 1982, Bienenstock, Cooper and Munro (BCM) proposed a concrete synaptic modification hypothesis in which two regions of modification (Hebbian and anti-Hebbian) were stabilized by the addition of a sliding modification threshold.

There are two ways to test a theory like that of Bienenstock, Cooper and Munro. One is to compare its consequences with experiment; the other is to directly verify its underlying assumptions. Recently two such avenues of research have supported this model of plasticity. Physiological experiments have verified some of its basic assumptions, while analysis and simulations have shown that the theory can explain existing experimental observations of selectivity and ocular dominance plasticity in kitten visual cortex in a wide variety of visual environments and make testable predictions.

The BCM theory was originally created to explain the development of orientation selectivity and binocular response of neurons in various visual environments in kitten striate cortex, one of the most thoroughly studied areas in neuroscience. The research philosophy of our laboratory is to keep our model of the cortex as simple as possible, and add details after behavior and consequences have been thoroughly understood. In this paper we will present a more realistic representation of the previous simplified visual environment. Effects on our previous findings, and the additional ways the extension allows further comparisons with visual cortex will be examined.

Research in this area began with Nass and Cooper (1975) who explored a model in which the modification of visual cortical synapses was Hebbian; i.e. a change to a synapse was based on the multiplication of the pre- and postsynaptic activities, and stabilization of the synaptic weights was produced by stopping modification when the cortical response reached a specified maximum — thus tying local modifications to the total cortical response. The idea that the sign of the modification should be based on whether the postsynaptic response is above or below a threshold was incorporated by Cooper et al. (1979) (see Fig. 1) to explain variations in selectivity with different visual environments. To stabilize the synapses without having to impose external constraints on them, the threshold was allowed, by Bienenstock et al. (1982), to slide as a non-linear function of

CONTRIBUTED ARTICLE

Unbiased Estimate of Generalization Error and Model Selection in Neural Network

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Abstract—*Model selection is based upon the generalization errors of the models in consideration. To estimate the generalization error of a model from the training data, the method of cross-validation and the asymptotic form of the jackknife estimator are used. The average of the predictive errors is used to estimate the generalization error. This estimate is also used as the model selection criterion. The asymptotic form of this estimate is obtained. Asymptotic model selection criterion is also provided for the case when the error function is the penalized negative log-likelihood. In the regression case, it also proves the asymptotic equivalence of Moody's model selection criterion and the cross-validation method under a condition on the error function.*

Keywords—Asymptotics, Cross-validation, Generalization error, Jackknife estimator, Kullback–Leibler measure, Model selection.

1. INTRODUCTION

Due to the flexibility and capability of neural network in modeling the underlying nonlinear functional relation or decision (Barron & Barron, 1988; Hinton, 1989; White, 1989; Hornik, Stinchcombe, & White, 1989), it is popular to use it in data analysis and AI research. One usually starts with a probability description of the process, and then parametrizes the probability model by a neural net function and at the same time introduces a prior distribution on the weight of the neural net and other parameters in the probability model. We shall refer to the term *model* in a general sense as the parametrized probability model including prior probability.

Various forms of error functions can be used to estimate the parameter in a model. However, it is more important to select the right model with small generalization error based on the training data set. Model selection is the topic of this article. In Section 2, we introduce the definition of the generalization error and use the method of cross-validation (Stone, 1974) to estimate it. This estimate is unbiased and is used as the model selection criterion. In Section 3, an asymptotic form of the jackknife estimator (Miller, 1974) is provided to reduce the computational costs incurred in the cross-validation method. In Section 4, the asymptotic form of the model selection criterion is given. In Section 5, the asymptotic model selection criterion is provided for the case when the error function is the penalized negative log-likelihood function; Akaike's Information Criterion (AIC) (Akaike, 1973) and Moody's extension (Moody, 1992) in the regression case are also discussed. It also shows that the asymptotic equivalence between Moody's model selection criterion and the method of cross-validation when the distance between the response y and the regression function is measured by the square of their difference.

2. GENERALIZATION ERROR AND ITS UNBIASED ESTIMATE

There has been a substantial amount of work in the problem of model selection (Lindley, 1968; Mallows, 1973; Akaike, 1973; Stone, 1974; Atkinson, 1978; Schwartz, 1978; Craven & Wahba, 1979; Zellner, 1984; MacKay, 1991; Moody, 1992). One way to assess the goodness of a model is through the Kullback–Leibler measure (Kullback & Leibler, 1951). Denote the underlying conditional probability distribution as

Organization of Receptive Fields in Networks with Hebbian Learning: The Connection Between Synaptic and Phenomenological Models

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Abstract

In this paper we address the question of how interactions affect the formation and organization of receptive fields in a network composed of interacting neurons with Hebbian type learning. We show how to partially decouple single cell effects from network effects, and how some phenomenological models can be seen as approximations to these learning networks. We show that the interaction affects the structure of receptive fields. We also demonstrate how the organization of different receptive fields across the cortex is influenced by the interaction term, and that the type of singularities depends on the symmetries of the receptive fields.

1

LTP, LTD and Cortical Receptive Fields: What do they tell us about Synaptic Modification ?

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1 Introduction

Receptive fields in the visual cortex of cats are dramatically influenced by the visual environment (For a comprehensive review see, Frégnac and Imbert, 1984) . In normally reared animals, the population of sharply tuned neurons increases monotonically, whereas for dark reared animals it initially increases, but then almost disappears (See, for example, Imbert and Buisseret, 1975). Ocular dominance is dramatically influenced by such manipulations as monocular deprivation (Wiesel and Hubel, 1963) or reverse suture (Blakemore and Van-Sluyters, 1974; Mioche and Singer, 1989).

These striking variations are generally believed to be the result of experience dependent synaptic modification.

Now there is also evidence that LTP (long thought to be a possible physiological substrate of memory) and LTD occur in a similar fashion in hippocampus and many areas of mammalian cortex (Kirkwood et al., 1993). It seems quite possible therefore, that LTP and LTD are manifestations of the same phenomena of synaptic change as those assumed to be taking place in visual cortex and that all of these involve similar modifications of synaptic efficacy: the physiological basis of learning and memory.

Many different synaptic modification rules have been proposed over the years - both to explain how cortical receptive fields evolve and to account for learning and memory storage in general (for example von der Malsburg 1973, Nass and Cooper 1975, Peres et. al. 1975, Bienenstock et. al. 1982 ,Linsker 1986, Miller 1994a).

In this paper we begin an attempt to distinguish between these rules - to explore to what extent they lead to results in agreement or disagreement with experiment. Although it has been stated that the precise form of the learning rule is not important - that any stabilized Hebbian modification rule leads to more or less the same conclusions - our results show that this is not correct. Furthermore, these statements are misleading; the details of the learning

1